HILGARDIA

A Journal of Agricultural Science Published by the California Agricultural Experiment Station

VOL. 31 DECEMBER, 1961 No. 16

BIOLOGICAL CONTROL OF WESTERN GRAPE LEAF SKELETONIZER (HARRISINA BRILLIANS B. and McD.) IN CALIFORNIA[1,2]

CURTIS P. CLAUSEN[3]

INTRODUCTION

THE LARVAE of the western grape leaf skeletonizer (*Harrisina brillians* B. and McD.) feed upon the foliage, and to some extent on the fruit also, of wild and cultivated grape. The natural distribution of the species covers Arizona, New Mexico, Texas, Utah, Colorado, and the Mexican states of Sonora and Chihuahua. It was first found in southwest San Diego County, California, in 1941, and in a short time threatened to become a serious pest in the commercial vineyards in that area. In 1942 the infested area was put under quarantine; movement of untreated fruits and grape stumps was prohibited and methyl bromide treatment of fruit containers was required. Crop losses in certain vineyards reached 90 per cent in 1943 and averaged 40 to 60 per cent.

Because of threat to the more extensive grape-growing areas to the north, the State Department of Agriculture initiated an eradication campaign in 1946. All infestations of cultivated grape were dusted with cryolite 50, in talc, at the rate of 25 pounds per acre, and wild grape in the Coast Range canyon areas was largely eliminated by applications of 2,4-D in a 15-mile barrier zone on the north and east. In 1951, when it became apparent that eradication was not possible, the objective was changed to a holding program, with continuation of the barrier zone. As a result of the great decline in the number of infestations from 1952 onward, the holding program was dropped in 1955, although a survey, including scouting of the peripheral area, continued to 1956 (see annual reports, Bureau of Entomology, in California State Department of Agriculture Monthly Bulletins, 1946–1956). The eradication and holding campaigns involved an expenditure of more than $800,000 over an eleven-year period.

---

[1] Submitted for publication April 27, 1961.

[2] Paper No. 1318, University of California Citrus Research Center and Agricultural Experiment Station, Riverside.

[3] Professor of Biological Control and Entomologist in the Agricultural Experiment Station, Emeritus, Riverside.

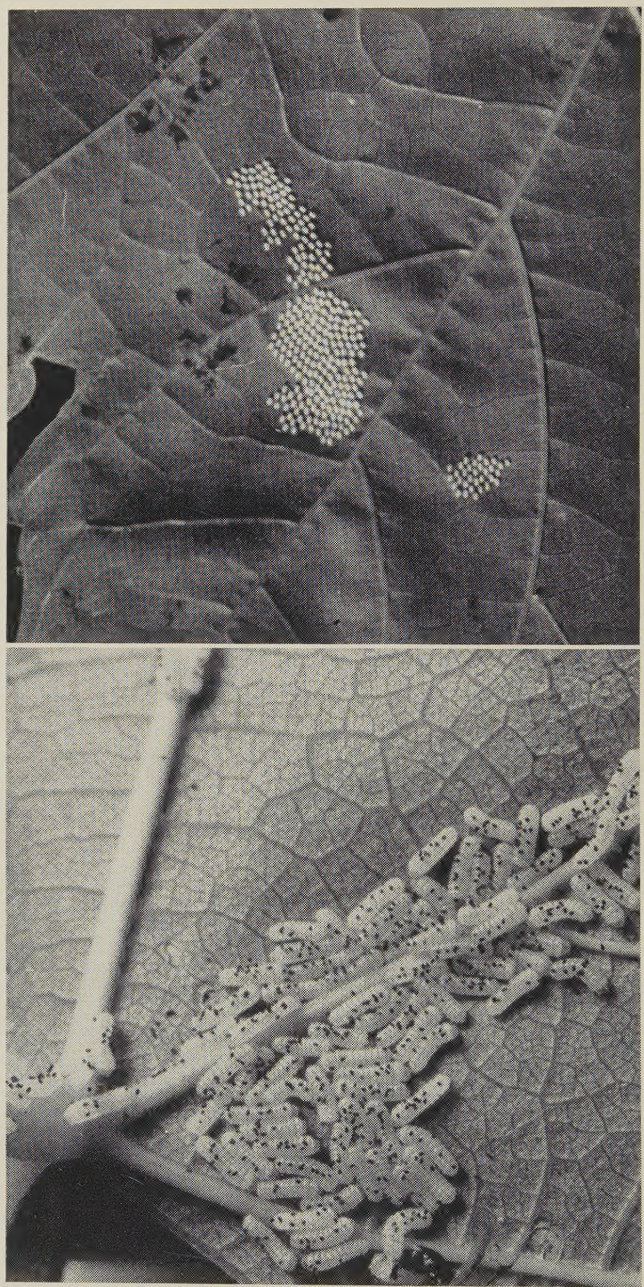

Fig. 1. Egg cluster (above, enlarged × $1\frac{1}{2}$) and colony of first-instar larvae (below, enlarged × 5), of *Harrisina brillians* B. and McD.

The biological control project was started in 1950, one year prior to the abandonment of the eradication effort in favor of a holding program. The work in biological control was carried on in coöperation with the State Department of Agriculture and the Agricultural Commissioner of San Diego County. The parasite colonization program was necessarily handicapped by the thorough cryolite dusting of all infestations, but this was somewhat relieved in 1951 by the shift to a holding program. In addition, in 1953 a biological control area was set up in the southwest portion of the infested zone, extending from the coastal slope south of San Diego River to Coyote Canyon in the northeast. The search for effective natural enemies covered the years 1950 to 1952 and the entire program was completed early in 1956.

LIFE HISTORY AND HABITS OF HARRISINA BRILLIANS

The adult moths of the grape leaf skeletonizer are conspicuous because of their coloration, the wings and body being metallic blue, often shading into green. They also have a characteristic manner of flight. The eggs (fig. 1) are pale yellow, capsular in form, measure 0.60–0.65 mm, and are ornamented with fine surface reticulations. The first- (fig. 1) and second-instar larvae are white or yellowish-white, with black setae, and are commonly dotted with pellets of black excrement. They are strongly gregarious and feed side by side in conspicuous orderly rows. The older larvae (fig. 2) are about 12 mm long and bear black transverse bands against a yellow background on the first two thoracic segments and on seven of the abdominal segments. The gregarious habit is much less evident in the older larvae.

The initial observations on the biology and habits of the skeletonizer in Arizona were made by Wehrle (1939),[4] and these were supplemented by observations in California by Lange (1944). Wehrle reports at least three generations each year on cultivated grape in Arizona; moths first appear in the vineyards in May and early June. The feeding periods of the larvae of the three broods are June and early July, late July and August, and September. Lange reports that this pest feeds on Virginia creeper and Boston ivy, in addition to wild and cultivated grape. The eggs, stated to be in clusters of up to sixteen or more, are laid on the under sides of the leaves. Some hibernating pupae are said to carry over to the second season.

Later observations during one season in southern California by Robinson (1950) revealed two full generations each year. About 3 per cent of the pupae of the second generation yielded adults during the autumn, but these probably failed to reproduce. Emergence of the first brood of adults in the spring coincides with the appearance of the first fresh grape foliage. Oviposition takes place 1 to 4 days after mating, and all eggs from each female are deposited within a day or two. Contrary to Lange's laboratory observations on the size of egg clusters, Robinson found that those deposited under field conditions contained up to 300 or more eggs (fig. 1), with an average of about 155. Those of the first generation hatch in 16 days and those of the second generation in 10 days. The larvae of the first three instars feed only on the surface tissue of the under sides of the leaves, leaving a characteristic

[4] See "Literature Cited" for citations referred to in the text by author and date.

Fig. 2. Fourth-instar larvae of *Harrisina brillians* B. and McD. (enlarged × 3).

network of fine veins, whereas those of the last two instars consume the entire leaf except the main veins and, in heavy infestations, may also feed upon the fruit. The pupal stage of the first generation is complete in 20 days and that of the second generation in 16 days. The pupae pass the winter encased in dirty-white silken cocoons in protected places, such as under loose bark or in rubbish beneath the vines.

The more extensive studies by O. J. Smith (unpublished notes) in southern California covered a period of five years and revealed a number of points in the life history of the skeletonizer differing from those reported by the earlier investigators. Under optimum summer conditions the larval stage is completed in about 3 weeks and the pupal stage in 10 to 13 days, the entire cycle from egg to adult covering 31 to 34 days. The peak of larval populations in the vineyards is attained in late July and extends through September, with the broods overlapping.

Normally there are two generations and a partial third each year in southern California, though the third is small in numbers during most seasons. A variable portion of the pupae of the second generation goes into diapause. In the experimental vineyard at El Cajon in 1954, 75 per cent of the pupae went into diapause. This was an exceptionally high figure, though still much lower than that indicated by Robinson. The reproduction of the third generation during the autumn months is governed by the amount of green foliage available as food for the larvae.

Harrisina metallica Stretch, which is distinguished by an orange-red collar on the pronotum, was found in some numbers among the collections

made in Arizona, and has appeared occasionally in the California collections. The ratio to *H. brillians* in California is about 1:1,500, whereas at Phoenix, Arizona, *H. metallica* may be dominant. Rearing and cross-breeding experiments have shown that *metallica* is merely a Mendelian variant of *H. brillians* (Langston and Smith, 1953).

Most of the known species of *Harrisina* occur in South America, yet the range of *H. americana* (Guer.), also a pest of grape, covers most of the eastern half of the United States. The climatic factors that limit the spread of *H. brillians* are not well understood, but the occurrence of heavy infestations in southern Utah indicates that climate would not serve to prevent spread of this pest into any of the principal grape-growing areas of California.

EXPLORATION FOR EFFECTIVE NATURAL ENEMIES

The out-of-state exploration for natural enemies of the skeletonizer that might aid in the control of the pest in California began in 1950 (Smith, 1953, 1954), when O. J. Smith and R. L. Langston conducted a search in Arizona and the adjoining Mexican states of Sonora and Chihuahua. A temporary field station was established at Ft. Huachuca, Arizona, and was used as a base of operations from June through October. The survey covered the southern half of the state and initially was limited to a search for infestations on wild grape in the mountain canyons. However, this search met with little success. Reports of past infestations on cultivated grape were received, and a shift in the area of search revealed heavy though small infestations of *Harrisina brillians* in vineyards at Emery Park in the Santa Cruz Valley and at Pomerene on the San Pedro River. Thompson Seedless appeared to be the grape variety most subject to heavy attack. Grape growers reported that the skeletonizer was sporadic in its appearance; it might be abundant for one or two years and then almost completely absent for several years following. The tachinid parasite, *Sturmia harrisinae* Coq., was present in all collections, whereas *Apanteles harrisinae* Mues. emerged from only three collections, all from Cochise County, situated in the extreme southeastern portion of the state.

Later in the same season, *Harrisina brillians* was found to be a serious pest in commercial vineyards at Delicias, Chihuahua, Mexico, but collections of larvae yielded no parasites other than an occasional specimen of *Sturmia harrisinae*. Bacterial and virus diseases, to be mentioned later, occurred frequently at Hermosillo, and collections of larvae from this locality, some of which undoubtedly were infected, apparently led to the initial outbreak of disease in the skeletonizer stocks being reared in the laboratory at Ft. Huachuca. The two parasites mentioned above were propagated in the laboratory and the stocks taken to the field station at La Mesa, California, later in the year for further production. The field collections, comprising approximately 40,000 host larvae, were stored outdoors through the winter in the Huachuca Mountains at an elevation of 8,000 feet, and yielded 6,004 adults of *H. brillians*, 593 *Sturmia*, and 7,177 *Apanteles* upon emergence at La Mesa the following spring.

Further investigations were undertaken in Mexico in 1951 and 1952. The

area covered extended from Mexico City and Vera Cruz northward to the American border, within which area thirteen species of *Harrisina* had previously been recorded. Two species of *Harrisina* were found in the Rio Blanco Valley, Vera Cruz, but *H. brillians* was scarce. A related zygaenid, *Malthaca* sp., was present in some numbers and collections of larvae provided 482 cocoons of *Apanteles* sp. B for shipment to California. This parasite was also found in the state of Michoacan. *H. brillians* was abundant in Chihuahua and collections at this time yielded *Apanteles harrisinae, Haltichella* sp., and two species of Tachinidae, all in small numbers. Here, also, *Dibrachys* sp. was found. Previously observed in Arizona, *Dibrachys* sp. is a gregarious parasite not only of *Harrisina* pupae but also of *Apanteles* larvae in their cocoons and of tachinid pupae. These, of course, were destroyed. Search on the west coast of Mexico, in the states of Colima, Jalisco, and Nayarit, failed to yield any species of Zygaenidae.

Additional collections, numbering 20,000 larvae, were made in Arizona in 1952, from which there emerged the following spring 2,933 *Apanteles harrisinae,* 648 *Sturmia harrisinae,* and 24 *Phorocera* sp. (near *tachinomiodes* Tns.).

Neither *Sturmia* nor *Apanteles* was abundant in any of the collections made in Arizona during the three-year period. The maximum for *Sturmia,* the more common of the two, was 24 per cent in an unsprayed vineyard at Globe. Most collections showed parasitization of less than 10 per cent.

During July to September, 1951, Harold Compere conducted a search extending from Missouri eastward to New York and south through the coastal states to Florida. Small and sporadic infestations of *Harrisina americana* had been reported from time to time in vineyards and on dooryard vines throughout this area. No infestations were found at any point, though occasional small colonies of that or other species of the genus were found on wild grape. Twenty-one small shipments of larvae were made to California, four of these by J. O. Pepper of Pennsylvania State University. Parasite emergence from these shipments was small, with the exception of one lot of a related zygaenid, *Acoloithus* sp., from Florida, which yielded 62 *Pelecystoma harrisinae* (Ashm.). An occasional individual of this species emerged from Illinois material also. Other rearings from these shipments included a few *Phorocera* sp., *Sturmia* sp. (probably *harrisinae*), and a solitary and a gregarious *Apanteles,* the latter probably *A. harrisinae.*

A further search was made in Louisiana and Florida by S. E. Flanders during August to September, 1952. Nothing was found in Louisiana, while in Florida the infestations of *Harrisina* and *Acoloithus* on wild grape were small and localized, as noted by Compere the previous year; 100 to 200 larvae per day was the maximum collection record. Nineteen air shipments sent to California yielded 60 *Pelecystoma harrisinae,* 93 of a solitary and a gregarious *Apanteles,* 62 tachinid flies of two species, and 100 *Haltichella* sp.

The scarcity of *Harrisina americana* in the eastern states during 1951 and 1952 indicates that it is now much less common than in the past. Numerous previous reports, especially that of Jones (1909), recorded that it was frequently injurious to garden vines, requiring insecticidal treatment, although it was not a serious pest in commercial vineyards.

A collecting trip to St. George, Utah, by O. J. Smith and the writer in September, 1953, revealed an exceedingly heavy infestation in a small abandoned vineyard. *Sturmia* adults were seen abundantly in this vineyard, actively engaged in attack upon the skeletonizer larvae. Fifteen thousand third- and fourth-instar larvae were collected and brought to Riverside for parasite rearing. Dissections showed parasitization by *Sturmia* to be 56.4 per cent. This collection was made well before the parasite had completed its attack on the host brood. Samples of hibernating larvae taken the following March showed parasitization of 72 per cent, demonstrating the capacity of the species to attain a high level of attack under favorable conditions. Because of the heavy larval populations of the preceding September, it had been anticipated that large collections of hibernating material could be obtained at this time. For unknown reasons, however, very few hibernating skeletonizer pupae were found. The cause of this disappearance could not be explained. The vineyard was completely free of infestation during the following seasons. No *Apanteles* were present in either of the St. George collections.

Insectary tests in California of all parasite species obtained from *Malthaca* and *Acoloithus* showed them to be fully adapted to *Harrisina brillians*.

INSECTARY PRODUCTION OF PARASITES

The development of economical production methods for both host and parasites was essential in order to provide adequate stocks of the latter for completion of the field distribution program (Smith and Langston, 1953; Langston, 1954). As indicated earlier, in the field in southern California, *Harrisina brillians* has two full generations and a possible third each year, and is in diapause for 6 months or more from autumn to the following spring. The principal parasites are also in diapause during this period, *Sturmia harrisinae* as a first-instar larva in the host and *Apanteles harrisinae* as a full-grown larva in its cocoon. Thus the problem was the production of food-plant foliage throughout the year and the manipulation or the prevention of diapause in the host and its principal parasites (Smith and Langston, 1953).

The initial stocks of overwintering host and parasite cocoons were brought to California late in 1950, after being exposed for 3 weeks to normal winter temperatures and to some precipitation in the Huachuca Mountains in Arizona. This was followed by a 2-months' warm-up period, with exposure to frequent precipitation, at La Mesa, after which the cocoons were brought into the insectary and subjected to summer temperatures. This combination of conditions resulted in heavy emergence of both host and parasites within 20 to 25 days and nearly 100 per cent emergence within a relatively short period. This breaking of the diapause of field-collected material, with adult emergence several months in advance of the normal date, made possible the production of two and one-half generations of the parasites in the insectary before the spring brood of adults of *Harrisina* appeared in the field. The 1952 importations of 20,000 cocoons from Arizona and 10,000 from Mexico were similarly treated.

The prevention of diapause in insectary stocks of *Harrisina brillians* was accomplished by provision of a consistent 15 hours of daylight each day.

Normal daylight was augmented when necessary by artificial illumination of a minimum intensity of 10 foot-candles and a maximum of 80 foot-candles, the amount dependent upon the location of the vines on the benches. Supplementary light was provided by a series of 150-watt incandescent bulbs wired to an automatic time switch. Under these conditions, *H. brillians* developed throughout the year without the appearance of diapause at any time. Thus, it appears that photoperiod is the main and probably the only environmental factor controlling diapause in this insect. Since the diapause of the first-instar larva of *Sturmia harrisinae* is correlated with that of the host pupa, the prevention of diapause in the host also prevented it in the parasite. *Apanteles harrisinae* likewise reproduced throughout the year without diapause under the conditions provided.

For production of host-plant foliage to maintain the skeletonizer throughout the year, the Thompson Seedless variety proved to be more satisfactory than other cultivated grapes or wild grape. Rooted cuttings were planted in 10-quart galvanized pails and grown in the greenhouse at summer temperatures. When the maximum of foliage had been produced, the plants were placed in a large artificially lighted room and exposed to oviposition by mated skeletonizer females. When optimum oviposition had taken place, the vines were removed to greenhouse benches where the larvae were permitted to feed until the fifth instar was attained. Production averaged 200 fifth-instar larvae per vine under these conditions. Later, it proved to be more efficient and economical to utilize cut shoots rather than potted plants in this program. These shoots were exposed for 24 hours to gravid moths and the leaf sections bearing egg clusters then removed and set aside for incubation of the eggs. These were then placed upon freshly cut shoots in trays just before hatching. Fresh foliage was provided at intervals when necessary until completion of larval feeding and development.

In the rearing of *Sturmia harrisinae*, the early fifth-instar skeletonizer larvae were transferred from the host-production room to large open trays equipped with hot-wire barriers and provided daily with cut grape foliage. These trays were than placed in a parasitization room in which mated flies were released. The bottoms of the trays were lined with corrugated cardboard, under which the skeletonizer cocoons were later spun. At the time of emergence no provision was necessary for separation of host and parasite adults, since the parasites completed emergence before issuance of the hosts.

The production of *Apanteles harrisinae* required exposure of the late first- and second-instar larvae on growing foliage. Nine to twelve potted vines, bearing 2,000 or more larvae each, were placed in a small parasitization room and exposed to 50 parasite females. When the host larvae had reached the fifth instar, they were transferred to glass wire-covered cages, $20 \times 20 \times 24$ inches, which were lined along the bottom with corrugated cardboard. Here they were fed with cut foliage until cocooning by the host. One thousand to fifteen hundred larvae were placed in each cage. For emergence of the adults, the cocoon material was placed in a cage, $4 \times 4 \times 6$ feet, which was divided into two equal compartments by a horizontal window-screen separator and contained a window in the wall of the upper compartment. The screen confined the emerging skeletonizer moths to the lower half,

while the *Apanteles* adults could find their way into the upper section where they were then removed by aspirator through a sleeve-covered port. As many as 2,000 *Apanteles* were produced each day during 1951 until production was halted by a virus disease outbreak in the host rearing stocks. Insectary production of *Apanteles* sp. B was similar to that used for *A. harrisinae,* except that only first-instar hosts were used and provision for cocooning of the host and for separation of parasites and moths at emergence was unnecessary. The *Apanteles* cocoons are spun on the foliage.

Pelecystoma harrisinae was reared in cylindrical screen cages with metal rod supports, 18 × 36 inches, over potted grapevines infested with 100 or 200 second- to fifth-instar skeletonizer larvae. Several female *Pelecystoma* adults were placed in each cage. The supply of host larvae was replenished when required and the parasite "mummies" removed daily. Later, *Pelecystoma* was produced in a parasitization room similar to that used for *Apanteles.*

The initial stock of *Pelecystoma,* imported from Florida by H. Compere in 1951, was lost in the course of the disease outbreak early in 1952, but was replaced by new importations from the same source by S. E. Flanders during the late summer of that year.

Insectary production of all species was largely completed at the end of the 1953 season, aside from the provision of relatively small members of *Sturmia* and *Apanteles harrisinae* required for release in a few new peripheral infestations, as these two established species had then dispersed over almost the entire infested area. The great decline in field populations of 1953 and following years, and the cessation of spread of the skeletonizer, made it difficult to locate suitable new colonization sites.

Because of space and labor requirements for the rearing of *Harrisina,* involving the year-round production and maintenance of large numbers of potted grapevines and, even more important, the periodic loss of the skeletonizer stocks through disease outbreaks such as occurred during 1951 and 1952, an effort was made to find one or more alternate host species better adapted to mass production and not subject to serious disease outbreaks. A considerable number of native foliage-feeding lepidopterous species available in adequate numbers in the field at certain periods of the year were tested to determine their suitability as substitute hosts for one or more of the parasite species. Also, certain other species, particularly amenable to large-scale insectary production and which had proved satisfactory in other parasite-rearing programs, were similarly tested. Among them were the potato tuberworm, *Gnorimoschema operculella* (Zell.), the salt-marsh caterpillar, *Estigmene acrea* (Drury), the Mediterranean flour moth, *Anagasta kühniella* (Zell.), and several others. The parasites of *Harrisina,* however, appear to be very restricted in their host preferences since they failed to reproduce on any of these species.

FIELD RELEASES

The first imported parasite to be released in California was *Apanteles harrisinae,* of which 670 adults were placed at Los Coches Creek in May, 1951. Total releases for that season to the end of August were 55,070 adults and

TABLE 1

FIELD RELEASES OF GRAPE LEAF SKELETONIZER PARASITES IN SOUTHERN CALIFORNIA, 1951–56

Species	Origin	Stage	1951	1952	1953	1954	1955	1956
Apanteles harrisinae	Arizona	Adults	55,070	......	2,787	500	300	600
		Parasitized host larvae	1,500	......	3,000	......	......	......
Apanteles sp. B	Vera Cruz, Mex.	Adults	......	......	14,793	......	......	......
		Parasitized host larvae	......	......	1,700	......	......	......
Pelecystoma harrisinae	Florida	Adults	779	......	12,063	......	......	......
		Cocoons	181	......	......	......	......	......
		Parasitized host larvae	......	......	900	......	......	......
Haltichella sp.	Chihuahua, Mex.	Adults	......	......	40	......	45	......
Compsilura concinnata	Connecticut	Adults	......	4,790	......	......	......	......
Phorocera sp.	Arizona	Adults	......	......	61	......	......	......
Sturmia harrisinae	Arizona	Adults	487	......	1,149	1,000	1,748	1,400
Total			58,017	4,790	36,493	1,500	2,093	2,000

1,500 parasitized host larvae at 28 colony sites. Insofar as possible, these adults were released on wild grape on which the host larvae were predominantly in the first instar. Because of the virus outbreak in the insectary during late 1951 and 1952, no stocks were available for colonization during 1952. In the meantime, both this species and *Sturmia harrisinae* had become established and spread in the field during 1951 and 1952, so that further releases were unnecessary except at a few outlying points. The stocks produced thereafter were utilized mainly in the experimental vineyard, which will be discussed later.

Initial colonization of *Sturmia harrisinae* took place in July and August, 1951, when 487 adults were released at ten colony sites in skeletonizer infestations predominantly of the fourth and fifth larval instars. Additional colonies were released at isolated sites and in the experimental vineyard during 1953 to 1956.

Pelecystoma harrisinae, originally obtained from Florida, was released at three sites during September to December, 1951, these colonies comprising 779 adults and 181 cocoons. The host stages attacked are the second and following instars, with the larger larvae preferred. These colonies were placed in localities well apart from those of the two parasites mentioned above, because of the possibility of loss through competition. An additional 12,063 adults and 900 parasitized host larvae were released in 1953 in infestations on wild grape in the canyons in the eastern portion of San Diego County and in the experimental vineyard.

Release of parasite colonies in remote mountain canyons, where wild grape was frequently common and known to be infested with the skeletonizer, was often difficult because of the rugged terrain that had to be traversed to reach the infestation sites. In some instances the colonies were packaged in conical hardware-cloth cages and dropped by signal flare chutes from a helicopter.

Apanteles sp. B was colonized only in 1953, when 4,200 adults were released in infestations on wild grape in several canyons, and 10,593 adults and 1,700 parasitized host larvae were placed in the experimental vineyard.

It was thought that the tachinid fly, *Compsilura concinnata* (Meig.), which originally had been imported into the United States from Europe for use against the gypsy and browntail moths, might prove of value against the skeletonizer since it was known to attack many lepidopterous hosts, one hundred or more being recorded in North America. Accordingly, arrangements to obtain stocks for field release were made with the Federal Bureau of Entomology and Plant Quarantine, through P. B. Dowden of the New Haven, Connecticut, laboratory. Large consignments of puparia, totaling 9,367, were received during late June and early July, 1952, and from these 4,790 adults became available for field release. Laboratory tests showed ready attack on and normal development in skeletonizer larvae. These adults were released, not only in skeletonizer infestations, but in those of the imported cabbageworm, *Pieris rapae* (L.), salt-marsh caterpillar, *Estigmene acrea*, and others. The seasonal cycle of *Harrisina brillians* is such that *Compsilura* cannot pass the winter in that host, consequently other hosts that hibernate in the larval stage are required to carry it over the winter and spring period.

The remaining two species of parasites, *Phorocera* sp. and *Halfichella* sp., were released in numbers too small to allow them to become established.

The total numbers of imported parasites released in California from 1951 to the completion of the program are given in table 1.

The entire parasite colonization program was much hampered, though unavoidably so, by the eradication program conducted by the State Department of Agriculture, during which cryolite dust was applied to all infestations, and wild grape in accessible canyons was eliminated by 2,4-D applications. This brought the infestations in all areas of the county to a low level, and consequently favorable sites for parasite releases with adequate populations of larvae were seldom available. Field surveys showed a marked reduction in the total number of infestations, due mainly to the dusting program; the number was 475 in 1952, 46 in 1953, 32 in 1954, and 28 in 1955. In 1953, the biological control area, comprising the coastal strip of San Diego County south of the San Diego River, was set up. The eradication program, later modified to one of preventing spread, centered on the periphery of the infested area to the north and east.

THE EXPERIMENTAL VINEYARD

During 1953 and 1954 a commercial vineyard of 6.6 acres of Thompson Seedless vines at El Cajon (fig. 3) was leased for experimental purposes. This was necessary because infestations in readily accessible areas had subsided so rapidly that it was difficult to test parasite increase in the field, the effect of competition between parasite species, and the effect of applications of sulfur for powdery mildew upon the parasite populations. For 1953, the vineyard was divided into three plots, one receiving no sulfur; the second, one application; and the third, two applications. The two applications, at the rate of 11 pounds of dust per acre, were made when the shoots were approximately 6 and 18 inches long.

The first requirement was to build up the skeletonizer population in the vineyard, and the initial releases in the spring consisted of 100 *Harrisina* larvae placed on each fifth vine in each fifth row. Adults were released at four points in each plot. These spring releases comprised a total of 18,300 larvae, 1,783 adults, and 500 egg masses. The infestation was still low by the middle of the summer, necessitating additional releases of 26,650 larvae, 3,462 adults, and 1,444 egg masses. It was difficult to obtain a satisfactory infestation in the vineyard because of a virus epizoötic that developed in mid-September in the centers of highest larval density. All larvae were killed on many vines.

Parasite releases were begun early in the season and continued as long as suitable host stages were available for attack. For the entire season, the releases totaled 1,099 adults of *Sturmia harrisinae;* 2,783 adults of *Apanteles harrisinae* and 3,000 parasitized host larvae; 10,593 adults of *Apanteles* sp. B and 1,700 parasitized host larvae; 7,338 adults of *Pelecystoma harrisinae* and 900 parasitized host larvae; 59 adults of *Phorocera* sp.; and 40 adults of *Haltichella* sp. At the end of the season large samples of overwintering cocoons showed 21.5 per cent parasitization by *Sturmia*, 16.2 per cent by *Apanteles harrisinae*, 2.2 per cent by *Apanteles* sp. B, and 0.6 per cent by *Pelecystoma*, or a total of 40.5 per cent. An additional 1,000 *Sturmia* adults were released in the vineyard in the spring of 1954.

In 1954 the skeletonizer populations were still low in the first generation

Fig. 3. The experimental vineyard at El Cajon, San Diego County, with parasite cages shown at right.

but high in the second. Seventy-five per cent of the larvae of the latter generation entered diapause. A heavy third generation population developed, but failed to progress to larval maturity because of a virus epizoötic. In 1955, as in the preceding year, the virus took a heavy toll of the larvae of the late generations, not only in the experimental vineyard but in many other areas as well. Virtually all eggs deposited during the heavy flight of moths in late August failed to hatch, due to disease, the effect of which was accentuated by unusually high temperatures at that time.

The application of sulfur dust is essential in commercial vineyards for control of powdery mildew. This apparently has no detrimental effect on moth reproduction, as populations were higher in dusted plots. The effect upon the parasites was uncertain, so studies covering this point were made in the three plots. It was known that with some hymenopterous parasites the ovipositional activities of the females are reduced or inhibited by sulfur dust, due to impaired functioning of the sensory organs on the antennae. The differences in parasitization by the several species, as determined by samples of overwintering cocoons of 1953–54, are shown as follows:

Species	No sulfur	One sulfur application	Two sulfur applications
	per cent	*per cent*	*per cent*
Sturmia harrisinae	20.6	22.5	21.3
Apanteles harrisinae	30.5	8.6	17.7
Apanteles sp. B	8.4	0.7	2.0
Pelecystoma harrisinae	1.3	0.5	0.6
Total	60.8	32.3	41.6

The figures for *Apanteles* sp. B and *Pelecystoma* are too low to be of any significance, and the failure of either one to become established in any locality indicates that other adverse environmental factors had a decisive influence upon them.

This and other tests revealed that *Sturmia* is affected little if at all by sulfur dust, whereas *Apanteles harrisinae* suffers severely, the effects persisting for about 3 months after application. This is not shown fully by the above figures, as there was a rapid build-up during the latter part of the season after the sulfur had disappeared from the foliage.

In 1954 infestations were highest in the sulfur-dusted plots, with about six times as many vines defoliated as in the undusted plot. Skeletonizer cocoons collected in October showed parasitization by *Sturmia* to be 26.3 per cent in the dusted and 24.8 per cent in the undusted plots; the comparable figures for *Apanteles harrisinae* were 26.2 and 37.7 per cent. These figures show that *A. harrisinae*, which had been seriously affected by the sulfur dust applications early in the season, had largely recovered from its earlier reduced status. The aggregate parasitization at the end of the season was thus 52.5 per cent in the dusted plot and 62.5 in that not dusted. The mean figures for the season were 33.5 and 56.5 per cent, respectively.

Heavy road dust on the foliage in some plots in the vineyard produced no apparent detrimental effect upon either parasite species.

Cryolite dusting, as practiced by the State Department of Agriculture for skeletonizer control outside the biological control area, proved to be highly destructive to both parasites. *Sturmia* parasitization of surviving larvae in the canyons surveyed was reduced from an average of 36.7 per cent to 6.1 per cent, and *Apanteles harrisinae* from 7.9 to 0.4 per cent.

The last survey of the infestation in the experimental vineyard was in June, 1956, at which time only 79 vines of the total of 2,038 were infested with skeletonizer larvae. All of these were in the plot that received three sulfur treatments the preceding season. This was a marked reduction from the 43.5 per cent infestation one year previously.

PARASITE RECOVERY STUDIES

Following the initial releases of *Sturmia harrisinae* in San Diego County during the summer of 1951, the collection of hibernating material from wild grape during the winter of 1951–52 showed establishment at all colony sites and a spread of at least 3 miles from one site. Parasitization was up to 14.9 per cent at Avocado Canyon. The 1952 summer generation at that site showed parasitization of 48.5 per cent, a rapid rate of increase. In the fall generation at Cat Canyon the parasitization of the same brood reached 64.9 per cent, and at Sequan Reservation, 50 per cent. In 1953, in the upland (above 600 feet elevation) the parasitization of the first generation on grape averaged 62 per cent at five sites, and in the second generation, 29.4 per cent. By this time, two years after initial release, dispersal of 13 miles from known colony sites was noted, although no skeletonizer infestations occurred in the intervening area. All areas checked that were not subject to cryolite dusting showed an average parasitization of 36.6 per cent, and those near colonization points, 52.9 per cent. The 1954 survey of infestations on

wild grape in the upland area showed parasitization ranging from 41 to 77.2 per cent, a substantial increase over the preceding year.

Recovery studies on *Apanteles harrisinae* demonstrated consistent establishment comparable to that of *Sturmia*. Collection of hibernating material during the winter of 1951–52 showed establishment at all colony sites except one, Sequan Reservation. At that time parasitization at Quail Canyon amounted to 50 per cent. The parasitization at Avocado Canyon was 20 per cent in the late months of 1951, 21.2 per cent in the 1952 summer generation, and 35.3 per cent in the autumn generation of that year. In Harbison Canyon parasitization for the last generation was 86 per cent; in Cat Canyon it was 23.5 per cent. In general, however, the high parasitization shown by *Apanteles* in several areas in 1952 was not maintained. The 1953 average for all sampled untreated areas was less than 10 per cent, and this situation persisted through the following years.

This decline in the field effectiveness of *Apanteles* came about in spite of the dominance of that species over *Sturmia* when in competition in the heavier skeletonizer infestations. The determining factor in this situation apparently was the differing degree to which the two species were subject to attack by secondary parasites.

The 1955 records from overwintering material showed that 57 to 90 per cent of the *Apanteles* was destroyed by native secondary parasites, mainly *Dibrachys* sp. This secondary parasite is especially destructive to the overwintering brood of *Apanteles* larvae in their cocoons, which are exposed to attack over a period of 6 months or more and may therefore suffer parasitization by several generations of *Dibrachys*. This secondary parasite also attacks the pupae of *Sturmia*, but its destructiveness is much less serious, as the puparial stage of the tachinid covers a period of only 2 weeks or less. On the other hand, attack upon species of Tachinidae of different habit, such as *Phorocera* sp., obtained from Arizona and released in small numbers, might be equally as serious as upon *Apanteles*, since this tachinid passes the winter in the puparial stage.

The aggregate parasitization by *Sturmia harrisinae* and *Apanteles harrisinae* in untreated areas was 42 per cent in 1953; the figure increased to 65 per cent in ten canyons in 1954, with an over-all parasitization of 62 per cent in all such areas surveyed. *Sturmia* appears to effect its maximum parasitization at low or medium host densities, whereas *Apanteles* parasitization is highest in heavy infestations. From late 1952 onwards, however, high density host infestations became increasingly rare, due in large part to virus epizoötics, and this condition, in conjunction with heavy attack by secondary parasites, greatly reduced the population of *Apanteles* in relation to that of *Sturmia*.

Releases of the remaining five parasite species were largely unsuccessful. *Apanteles* sp. B was recovered at Alpine in the autumn of 1953 at the site of releases earlier that season, and also in the experimental vineyard at El Cajon, but did not persist. A few individuals of *Pelecystoma harrisinae* were likewise reared from autumn collections of that year at Alpine, El Cajon, and La Mesa, but failed to become established. The remaining species, *Compsilura concinnata*, *Phorocera* sp., and *Haltichella* sp., were never recovered,

the first in spite of relatively large numbers released on several hosts and the other two probably because of the small numbers available for colonization.

BIOLOGY AND HABITS OF THE PARASITES

Sturmia harrisinae Coq. (Tachinidae)

The tachinid fly *Sturmia harrisinae* is a solitary internal parasite of the larvae of *Harrisina*, of which it prefers the fourth and fifth instars, especially the early fifth, for initial attack (Smith, Dunn, and Rosenberger, 1955). To a limited extent it attacks also the second and third instars. In the out-of-state areas surveyed for natural enemies, it was encountered commonly only in Arizona and Utah, though a few specimens of what is assumed to be the same species were obtained from *H. americana* and *Acoloithus* sp. collected in Florida.

The first brood of flies emerges from mid-April to mid-May and later. Mating occurs very soon after emergence and embryonic development of the oldest eggs in the basal part of the ovarioles of the parent female is complete 3 to 4 days later. The *Sturmia* female is capable of producing about 300 eggs. A female may oviposit in ten or more hosts of a cluster within a few minutes, and it is therefore probable that her full quota of eggs is exhausted within a relatively short period if suitable hosts are available in abundance. Larviposition takes place mainly during periods of bright sunshine at midday. The sex ratio is approximately 1:1.

The fully developed first-instar larvae in choria are deposited on the body of the host (fig. 4), usually at one end or the other, since the host caterpillars array themselves in closely packed rows while feeding, exposing only the ends of the body to attack. The chorion of the egg is invariably broken at the moment of deposition and the young larva enters the host at a nearby point within 2 to 3 minutes.

The first-instar larva wanders about for a short time within the host body and then settles in the lumen of one of the silk glands. Here it remains, undergoing very little development, until the host larva transforms to the pupal stage, when the parasite leaves the disintegrating silk gland and makes an incision in the pupal integument near a prothoracic spiracle. It then applies its posterior extremity to this aperture, about which a respiratory funnel soon forms. The parasite larva retains its connection with this respiratory funnel through its entire feeding period. Larval development is rapid after attachment, and the host pupa is killed 3 to 4 days before the parasite larva attains maturity. It then ruptures the host integument at the juncture of the thorax and abdomen, and emerges. The puparium is always formed within the host cocoon, usually adhering to the collapsed remains of the host pupa, though often within the pupa and at its anterior end.

In the overwintering generation the diapause period of the first-instar larva may be much prolonged, covering up to 8 months, since it is governed by the duration of diapause of the host pupa. The duration of the puparial stage is also variable. Development goes on slowly at temperatures of 55° F and above, covering a period of 9 to 15 days at 70° F.

There are two generations each year, though the second may be incom-

Fig. 4. Female of *Sturmia harrisinae* Coq. preparing to oviposit in a fourth-instar larva of *Harrisina brillians* B. and McD. (enlarged × 4).

plete. When development proceeds uninterruptedly in the summer generation, the cycle from egg to adult may be completed in 32 to 35 days if initial attack is on fully grown caterpillars approaching the time for pupation. The second larval stage is very short and the third covers only about 1 week. In 1953, however, approximately 50 per cent of the first-instar larvae of the summer generation went into diapause, this being correlated with the diapause of the host.

Apanteles harrisinae Mues. (Braconidae)

The species *Apanteles harrisinae* is a gregarious internal parasite of the larvae of *Harrisina brillians* and was found most commonly in Cochise County, Arizona, though specimens were also reared from that host in Chihuahua, Mexico, and from related zygaenids in Florida. In the field the adults emerge from overwintering cocoons during May, about 6 to 19 days later than emergence of host moths. Mating takes place the day following emergence and oviposition begins 1 day later. The adult wasps are crepuscular in habit, the greatest ovipositional activity being in the subdued light of early morning and late afternoon. Attack upon host larvae is mainly on those of the late first instar, though oviposition and development may also be successful in second- and third-instar larvae. Five hundred or more eggs may be found in the ovaries of each female, and this number probably represents the oviposition capacity of the species. The ovipositor is inserted into the abdomen of the host larva, and 3 to 9 eggs deposited at each insertion. Thirty

Fig. 5. Cocoons of *Apanteles harrisinae* Mues. in opened cocoons of *Harrisina brillians* B. and McD. (enlarged × 3).

or more hosts may be attacked in rapid succession. Adult life of the female covers only about 4 days when free oviposition is permitted.

The incubation period is short and larval development, including spinning of the cocoon, is completed in about 18 days. The length of the cocoon stage is variable, a range of 13 to 34 days having been noted in a cluster from a single host larva. The minimum time needed to complete the cycle from egg to adult in the summer generation is 30 days. Because of this short life cycle, it is possible for the parasite to have several more generations each season than the two and partial third of the host. The full-grown larvae of *Apanteles* emerge from the full-grown host larva immediately after the latter has spun its cocoon. The cocoons are spun within that of the host (fig. 5) and surround the dead caterpillar. Up to 28 individuals may develop to maturity in a single host. The sex ratio from field-collected cocoons was approximately 1:1, as compared with 2:3 for insectary-reared stocks.

In multiple parasitization involving *Apanteles harrisinae* and *Sturmia harrisinae* the former is normally dominant, as is to be expected, inasmuch as *Apanteles* larvae attain maturity and emerge from the host larva shortly after the cocoon is spun, at which time the *Sturmia* larva is still of the first instar. Occasionally, however, both may reach maturity, in which case they both emerge from the prepupa, although the adults of *Sturmia* developing in this way are diminutive in size.

Apanteles sp. B (Braconidae)

The biology and habits of the parasite *Apanteles* sp. B, obtained from *Malthaca* larvae collected in Vera Cruz and Michoacan, Mexico, differ in

Fig. 6. Female of *Pelecystoma harrisinae* (Ashm.) ovipositing in fourth-instar larva of *Harrisina brillians* B. and Mc.D. (enlarged × 4).

several respects from those of *A. harrisinae*. Young skeletonizer larvae, usually of the first instar, are attacked and the full-grown parasite larvae emerge from second- to fourth-instar hosts rather than from the fifth instar in the cocoon, as is the case with *A. harrisinae*. The *Apanteles* sp. B cocoons are therefore found on the foliage rather than in the host cocoon. One to three may emerge from a second-instar host larva and up to eight from one of the fourth instar.

Pelecystoma harrisinae (Ashm.) (Braconidae)

The solitary internal parasite *Pelecystoma harrisinae* has been recorded as reared from *Harrisina americana* in the eastern states from Pennsylvania to Florida. The main stocks imported into California came from Florida, the host being a related zygaenid, *Acoloithus* sp. *Pelecystoma* attacks all larval instars (fig. 6) and develops to maturity in all except the first instar, though adults arising from second-instar hosts are exceedingly small and of low viability (Smith, Diboll, and Rosenberger, 1955). The largest and most vigorous reach larval maturity in fourth- and fifth-instar hosts. Within 12 days after parasite oviposition, the host larva ceases feeding and becomes flaccid, and the normal body color disappears, changing to light tan and and then to orange-pink. The entire body contents, except those of the head, are consumed. So complete is the feeding that even the conspicuous yellow

and blue pigments of the host, which lie in a loose layer of epidermis beneath the cuticle, are devoured. The transparent pupal capsule, or cocoon, is formed within the host skin and is of two distinct layers, the inner one having an opening at the posterior end through which the prepupal meconium is cast. The orifice is then sealed by the last larval exuvia. The meconium, therefore, lies between the two layers of the cocoon. The capsule is bathed in a pinkish-orange fluid derived from the parasite larva, which apparently serves to inflate the host skin. This fluid later dries out and the characteristic light-orange colored "mummy" is found clinging to the foliage by the tarsal claws or the crochets of the prolegs of the host.

At summer temperatures, the egg stage covers a minimum of 2 days; the larval stage, 6 days; and the pupal stage, 6 to 8 days. The average cycle from egg to adult is 14 to 15 days for the males and 16 to 17 days for the females. Unmated females produce only male progeny, whereas mated females yield both sexes. The normal sex ratio of field material is approximately 1:1.

Artificial manipulation of environmental conditions failed to reveal any tendency toward diapause in any stage of this species. Mummies exposed to temperatures of 45° and 50° F showed almost complete mortality in one week. This apparent lack of diapause, and the known occurrence of *Pelecystoma* as far north as Pennsylvania, would indicate that it may pass the winter in the adult stage.

The short life cycle of slightly more than 2 weeks would permit eleven or more generations to develop during the season, as against only two and a partial third for the skeletonizer.

MICROBIAL DISEASES OF THE SKELETONIZER LARVAE

The initial survey of the skeletonizer population in San Diego County failed to reveal the presence of any disease affecting the larvae. However, the field-collected material held in the temporary insectary at Ft. Huachuca, Arizona, during the summer of 1950 showed diseased larvae in the parasite-rearing rooms. The parasite stocks were transferred to La Mesa, California, in October of that year, and very soon thereafter, in the spring of 1951, the disease appeared among skeletonizer larvae being produced for parasite propagation. Samples of diseased larvae from Ft. Huachuca and La Mesa were submitted to E. A. Steinhaus for diagnosis and were found to contain a sporeforming bacillus, believed to be *Bacillus cereus* F. & F. Later examination of additional material revealed the presence of an apparently undescribed granulosis virus (Steinhaus and Hughes, 1952). The *Bacillus* is believed to be a secondary invader.

The occurrence of this virulent virus disease in California can almost certainly be attributed to unintentional introduction of contaminated host material from Arizona and Sonora to the laboratory at La Mesa, as it, as well as the *Bacillus,* was found commonly in field-collected larvae from both sources.

The two outbreaks of the virus disease in the insectary, following the advent of hot, humid weather in midsummer, were so severe that a large portion of the skeletonizer larvae being produced for parasite rearing died,

Fig. 7. Colony of fourth-instar larvae of *Harrisina brillians* B. and McD. killed by disease.

and the production program for late 1951 and 1952 was brought to an end. To solve the problem, it became necessary to destroy all host and parasite stocks and potted grapevines then held in the insectary and to completely disinfect the building and all equipment. This problem was studied by C. G. Thompson of the Department's Laboratory of Insect Pathology at Berkeley and methods were recommended for control of the outbreak. The insectary was first washed with hot water and soap and then with formalin. Equipment was autoclaved or dipped in formaldehyde. Thereafter, strict sanitation measures, including disinfection of the egg masses of the skeletonizer stock (immersion of the egg masses in 10 per cent formaldehyde for 2 hours) permitted resumption of the parasite production program on the required scale during 1953. The latter measure was not completely successful, as transovarial transmission of the virus within the egg was later demonstrated, but it reduced substantially the incidence of disease.

The virus first appeared in the field in San Diego County in the early summer of 1951 in Avocado and Quail Canyons, where *Apanteles* and *Sturmia* colonies derived from the Arizona collections had been released a short time earlier. Its rapid dissemination was also aided by release of contaminated insectary-reared parasites immediately before clean-up of the insectary became necessary in 1952.

After the virus became generally distributed in San Diego County, it was

observed that heavy field infestations of skeletonizer often died out completely. The only remaining evidence of the presence of large numbers of larvae were the small patches of parenchyma tissue, usually about 1 square inch, that had been eaten out by colonies of the young larvae before death. These distinctive "window-marking" feeding signs proved useful in detecting light infestations and in establishing the presence of the skeletonizer in isolated areas, even when living stages could not be found.

The external evidences of virus infection in the skeletonizer are (1) failure of the eggs to hatch and of the young larvae to feed, (2) abnormal larval feeding, and (3) abnormal growth, coloration, and eventual death of the larvae. Many young larvae spin down and die while still suspended by the silken thread. Diseased larvae tend to feed in a spotty manner, whereas healthy larvae feed in a compact group, consuming the leaf tissues over an ever-widening area. Most of the larger diseased larvae (fig. 7) finally drop to the ground, while others may be found clinging to the leaf by their prolegs. As the larva's feeding habits become spotty, the yellow integument gradually darkens, after which it turns dark brown and the body contents liquefy, desiccate, and finally turn black. The principal site of virus infection is the mid-gut epithelium.

Transovarial transmission of the virus was studied by electron microscope examination of eggs dissected from the reproductive system of moths issuing from diseased cultures and of laid eggs that had first been thoroughly sterilized externally. The results indicated strongly that such transmission does occur.

In the field it was noted from 1952 onwards that virtually disease-free skeletonizer larvae were available only from cryolite-dusted areas. This treatment almost eliminated the parasites, whereas, in areas where the parasite populations were building up rapidly, the disease was prevalent everywhere. These observations led to tests on the role of the two established parasites, *Sturmia harrisinae* and *Apanteles harrisinae,* in mechanical transmission of the virus. Adults were first permitted to wander about on foliage contaminated with diarrheic discharges of diseased skeletonizer larvae, after which they were caged with presumably disease-free larvae. The larvae exposed to *Sturmia* showed 38.5 per cent mortality and those exposed to *Apanteles* showed 25 per cent mortality, whereas the controls remained free of disease (Smith *et al.*, 1956). Had this role of the parasites in transmission of the virus been known earlier, its spread could have been expedited by exposing the colonies of adult parasites to a dust mixture or a liquid suspension of the virus prior to their release in the field.

The incubation period of the virus in skeletonizer larvae varies with the stage of development of the larvae. Tests were made in which healthy larvae of different instars were fed grape foliage that had been dipped in a virus suspension (filtrate of 100 diseased larvae macerated in 250 cc of water). These tests revealed that newly hatched larvae ceased feeding 9 to 19 days after ingestion of contaminated foliage. The first mortality occurred on the ninth day and 100 per cent mortality resulted after 31 days. With third-instar larvae, however, incubation of the virus was more rapid, 5 to 8 days elapsing to cessation of feeding, 6 days to first mortality, and 12 days to 100 per cent mortality.

The successful results attained in the use of the widely known *Bacillus thuringiensis* Berliner in laboratory and field tests against the larvae of a wide range of lepidopterous pests prompted a study of its possible usefulness against *Harrisina brillians* (Hall, 1955). A series of small field tests in 1952 and 1954 yielded results that were somewhat variable. One application against first-instar larvae resulted in 100 per cent mortality as compared with 30 per cent in the control. Another application against second- and third-instar larvae showed 46 to 75 per cent mortality, dependent on dosage, and 33 per cent in the control. A third test, using a Hi-Fog and garden sprayer against populations of larvae of mixed ages, showed mortalities of about 85 per cent, identical with those in the control. This last result was probably due to the widespread occurrence of the granulosis virus in both plots even before treatment. It was found that 25 to 30 per cent of the skeletonizer larvae displayed resistance to the bacillus when the food was saturated with a concentrated spore suspension. On the basis of these tests, it appears improbable that *B. thuringiensis* can be used effectively in the field control of this pest.

THE FINAL RESULTS

The biological control program against the western grape leaf skeletonizer has been an outstanding success, as evidenced by the great decline in number and size of infestations and a very marked slowing up of spread of the pest to new areas. The factors responsible for this outcome are the two larval parasites, *Sturmia harrisinae* and *Apanteles harrisinae*, imported from Arizona, and a virus disease that was accidentally brought in with host and parasite material from that state in 1950 to 1951. Unquestionably, the virus must be credited with the major role in reducing the pest to its present low population level and in exterminating many small infestations. It has not acted independently, however, as the parasites have played an important role in its dissemination from caterpillar colony to colony and from one area to another. As was to be expected, virus disease epizoötics developed most frequently in skeletonizer infestations of high population density.

It has been impossible to evaluate the efficiency of the parasites apart from that of the virus, as they became established and spread concurrently. Also, the general cryolite dusting program of the earlier years held skeletonizer populations at a low level, hampering or entirely preventing parasite activity and making it impossible to obtain adequate samples except in a restricted area. Percentages of parasitization figures are given as supporting evidence, but these, in themselves, have little meaning with respect to the degree of control attained. High figures, however, do have a value in that they show a ratio of populations favorable to biological control.

In general, field control in specific areas was attained within two years, while in others a three-year period was required. Both parasite species were effective at all host densities, though not equally so, and under favorable conditions were able to effect a general field parasitization of 65 per cent, with many collections exceeding that figure. The aggregate field parasitization in untreated areas in 1953 was 42 per cent, while in 1954 a survey of wild grape in ten canyons showed parasitization of 65 per cent or more.

Field surveys showed that the number of infestations discovered declined

consistently during the period covered by the project, from 472 in 1952 to 28 in 1955. In addition, 13 of the latter involved only single vines. Incipient infestations in 1955 showed a marked decline in larvae of the second generation and exceedingly small numbers or none at all in the third generation. Epizoötics of disease were general in the experimental and adjoining vineyards in both the first and second generations, with the result that practically all eggs deposited during the moth flight of August failed to hatch. The frequent finding of the characteristic feeding signs where no living stages of the skeletonizer were present emphasized the efficiency of the virus in reducing or eradicating small localized infestations.

Under natural field conditions, unhampered by insecticide applications, it was possible to follow the sequence of events in six widely separated canyons. In all of these, four stages were readily recognizable: (1) moderate to high host densities, (2) the appearance of the granulosis virus, (3) the gradual attainment of an aggregate parasitization by *Sturmia* and *Apanteles* of approximately 65 per cent, and finally (4) the virtual or actual disappearance of the skeletonizer.

Since the termination of the biological control program early in 1956, it has not been practicable to make extensive field collections to evaluate the continued effects of the parasites and the virus disease upon the skeletonizer infestations. There has been virtually no change in the field situation since that time, and a condition of equilibrium at a comparatively low level has been attained. Periodic field observations have been made by the members of the San Diego County Agricultural Commissioner's office. F. T. Thorne, Deputy Agricultural Commissioner, advises, on the basis of these observations and on reports of pest control operators, that only small but occasionally heavy infestations have appeared in semicommercial vineyards and back-yard plantings in recent years, particularly in the El Cajon district. Insecticidal treatments have been unnecessary for prevention of damage in commercial vineyards, although to comply with quarantine regulations, cryolite, DDT or methoxychlor dusting is still practiced by some growers as an alternative to fumigation of the crop after harvest.

The program for biological control, by greatly reducing the populations of the skeletonizer, has contributed to a reduction in the rate of spread of the pest in San Diego and Riverside counties. The main area of infestation has extended only once since 1955. The pest was discovered in 1960 near Escondido, about 10 miles west of the nearest previously known infestation. An infestation in residential plantings was found in June, 1961 at Kerman, Fresno County, more than 300 miles north of the southern California infestation. Establishment there must have resulted from transport of living stages into the area, rather than from natural spread.

ACKNOWLEDGMENTS

The late Owen J. Smith, Assistant Entomologist in the Experiment Station, was in charge of the grape leaf skeletonizer project throughout its development, and the present account has been prepared on the basis of his several published papers dealing with single phases of the project, and on his semiannual reports for 1950 to 1955, on file at the Citrus Research Center and Agricultural Experiment Station, Riverside. Unfortunately, his death in 1956 prevented the preparation of a comprehensive final report on the development and outcome of the project. All photographs are by him.

Invaluable assistance was rendered during the course of the project, especially in the insectary rearing program, by R. L. Langston, A. G. Diboll, and P. H. Dunn, Senior Laboratory Technicians, and by J. H. Rosenberger, Laboratory Technician, during various periods. A. J. Basinger assisted in the initial survey for natural enemies in Arizona in the spring of 1950.

Thanks are extended to the officials of the Mexican Secretaria de Agricultura y Ganaderia, especially those of the entomological center at San Jacinto, for much advice and assistance during the course of the explorations in Mexico, and to the Rockefeller Foundation in Mexico for laboratory space and facilities at their station at Chapingo.

The representatives of the California State Department of Agriculture, Bureau of Entomology, especially A. G. Forbes, Entomologist-in-Charge of the skeletonizer-eradication project, were extremely helpful at all times in the release of parasite colonies in remote canyons, the collection of samples for parasitization counts, provision for a biological control area in southwest San Diego County, and for the loan of the services of R. L. Langston from June, 1950, to June, 1951. San Diego County Agricultural Commissioner Dean Palmer and Deputy Commissioner F. T. Thorne provided invaluable assistance in many ways throughout the project.

Many entomologists in the eastern states gave valuable assistance in the search for natural enemies in that part of the country during 1951 to 1952. Special thanks are extended to J. O. Pepper of Pennsylvania State University, B. B. Pepper of Rutgers University, and G. W. Dekle of the Florida State Plant Board.

LITERATURE CITED

HALL, I. M.

1955. The use of *Bacillus thuringiensis* Berliner to control the western grape leaf skeletonizer. Jour. Econ. Ent. **48**(6): 675–77.

JONES, P. R.

1909. The grape-leaf skeletonizer (*Harrisina americana* Guerin-Maneville). U. S. Dept. Agr., Bur. Ent. Bul. **68**(pt. 8): 77–90.

LANGE, W. H. JR.

1944. The western grape leaf skeletonizer, *Harrisina brillians*, in California. California State Dept. Agr. Bul. **33**(2): 98–104.

LANGSTON, R. L.

1954. Methods for mass rearing of *Harrisina brillians* (Zygaenidae). Lepid. News **8**(1–2): 11–12.

LANGSTON, R. L., and O. J. SMITH

1953. Notes on the zygaenid genus *Harrisina* Packard, with special reference to *Harrisina metallica* Stretch. Ent. News **64**(10): 253–55.

ROBINSON, D. W.

1950. Description, life history and habits of the western grape leaf skeletonizer, *Harrisina brillians* B. and McD. California State Dept. Agr. Bul. **39**(3): 149–51.

SMITH, O. J.

1953. Grape leaf skeletonizer. California Agric. **7**(5): 9.

1954. Progress of the program to control western grape leaf skeletonizer with natural enemies. Blue Anchor **31**(2): 6–9, 44.

SMITH, O. J., A. G. DIBOLL, and J. H. ROSENBERGER

1955. Laboratory studies of *Pelecystoma harrisinae* (Ashmead) an adventive braconid parasite of the western grape leaf skeletonizer. Ent. Soc. Amer. Ann. **48**(4): 232–37.

SMITH, O. J., P. H. DUNN, and J. H. ROSENBERGER

1955. Morphology and biology of *Sturmia harrisinae* Coquillett (Diptera), a parasite of the western grape leaf skeletonizer. Univ. California Pubs. Ent. **10**(5): 321–58.

SMITH, O. J., K. M. HUGHES, P. H. DUNN, and I. M. HALL

1956. A granulosis virus disease of the western grape leaf skeletonizer and its transmission. Canad. Ent. **88**(8): 507–15.

SMITH, O. J., and R. L. LANGSTON

1953. Continuous laboratory propagation of western grape leaf skeletonizer and parasites by prevention of diapause. Jour. Econ. Ent. **46**(3): 477–84.

STEINHAUS, E. A., and K. M. HUGHES

1952. A granulosis of the western grape leaf skeletonizer. Jour. Econ. Ent. **45**(4): 744–45.

WEHRLE, L. P.

1939. Grape insects in Arizona. *In* Ariz. Agr. Expt. Sta. Bul. **162**: 274–92.

4*m*-12,'61 (C3411) A.M. 141